OBSERVATIONS ON BIRD DISTRIBUTION AND FEEDING ASSEMBLAGES ALONG THE RIO CALLARIA, DEPARTMENT OF LORETO, PERU

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This paper presents a summary of bird observations made in late July and early August, 1963, along the Rio Callaria, a small tributary of the Ucayali in the Department of Loreto, Peru. The Rio Callaria flows westward from the Brazilian border region to its confluence with the Ucayali at approximately 8°8′S and 74°38′W. From this point we travelled by dugout canoe some 20–30 miles upstream and returned. Observations of birds were made from the river and its banks and on excursions into the flanking forests. The relative abundance of 88 species in each of three distinct vegetational zones is given along with incidental notes and a description of two mixed assemblages of birds observed in feeding trees.

ECOLOGICAL ZONATION OF BIRDLIFE

So far as we were able to ascertain, the terrain in the vicinity of the Callaria had suffered relatively little from the effects of human incursion. Three small Indian villages with their adjacent plantations of bananas and yucca occupied high sections of the bank, thus creating small enclaves of secondary habitat. In addition we were informed by a missionary, who had lived a number of years in one of these villages, that some selective logging for "cedar" had taken place in the forests upstream during periods of high water. As "cedar" trees occur uncommonly and singly, the effects of this logging were not apparent. Thus the observations reported here, to a close approximation, should reflect the status of birdlife in an undisturbed primary region.

The distinctive feature of the Callaria is that natural habitats replace one another in a succession as one passes upstream. Thus, within a relatively short distance we had the opportunity to relate changes in bird distribution to an evident ecological zonation along the river.

In the course of its lower 20 miles, the Callaria flows through three distinct vegetational zones. The first of these is a low-lying flood-plain or matorral formation (MacBride, 1936) which extends upstream from the mouth for about 3 miles. The river runs nearly straight here and at the time of our visit was confined to a shallow channel about 100 feet in width. There was no forest within sight of the river in this stretch, the vegetation along its banks consisting of a dense growth of rangy bushes and tall grass.

The second, middle zone, a transitional region, extends for 5–8 miles above the flood-plain. Along this section the river becomes gradually narrower,

turns more frequently, and flows between progressively steeper banks as one proceeds upstream. Concommitantly, the character of the vegetation changes from that of the lower reaches to the high overhanging canopied forest typical of the upper river. In most of this transitional section the forest does not impinge on the banks but lies back somewhat. A bordering strip, up to 50 yards in width, of tall grass and/or dense shrubbery and bushes fills the intervening area.

In the third zone, further upstream, the forest closes in on the banks of the river, the channel becomes reduced to a width of 40–70 feet, and the stream flows rapidly. The overhanging trees are sufficiently tall to shade the water for much of the day. Numerous fallen trunks lying in the channel provide perches for hawks, kingfishers, swallows, and flycatchers.

By early August the dry season in eastern Peru is well advanced. Consequently, during our visit the river's flow was near the minimum for the year. Extensive sandy banks were exposed along most of its course, and in the lower section particularly there were many bars and shoals in mid-stream. During the rainy season, which extends from November to May, the Ucayali and its tributaries fill with water, the annual fluctuation in river level approaching forty feet in many places. Although we were told that there had been no rain for more than two months, the vegetation, except for a few species of deciduous trees, showed few signs of desiccation either close to the river or on higher ground. The high humidity, heavy dew each night, and low evaporation from the shaded forest floor are probably all important in maintaining the verdant aspects of this region throughout the dry season.

Table 1 summarizes our observations on the distribution of birds in the three vegetational zones. The relative abundance in each zone is given for 88 species of birds. Nomenclature follows that of de Schauensee (1966). Species that were regularly seen in pairs are denoted by a "p" in parentheses after the name. The only positive evidence of breeding activity that we obtained was a nest burrow containing a single white egg attributed to *Monasa nigrifrons* by our Indian guides.

A summary of the zonal distribution of the 88 species is presented in Table 2. The species in each zone have been classified according to whether they occurred in all three zones, in two, or only in the zone in question. Those found in all three must occupy niches that all three zones share in common, for example, the air space over the river.

The data in Table 2 suggest the following statements regarding the environmental factors controlling bird distribution on the Rio Callaria.

(1) The avifauna of the lower zone is by far the poorest in species but nevertheless is distinct to a high degree. Apart from the 11 wide-ranging forms (two storks, one vulture, one kingfisher, one puffbird, two flycatchers,

TABLE 1

LIST OF BIRD SPECIES OBSERVED ALONG THE RIO CALLARIA.

(The relative abundance of each species in the three vegetational zones is indicated as follows: +, 1–3 observations; ++, 4–10 observations; +++, more than 10 observations)

	Zone		
	Lower	Middle	Upper
Ardeidae			
Pilherodius pileatus		+	
Butorides striatus	++		
Casmerodius albus		+	
Tigrisoma sp. (p)			+
Ciconiidae			
Mycteria americana	+	+	+
Jabiru mycteria	+	++	++
Threskiornithidae			
Mesembrinibis cayennensis			+
Anhimidae			
Anhima cornuta (p)		+++	++
Cathartidae			
Sarcorhamphus papa			+
Coragyps atratus	+++	+++	+++
Cathartes aura		++	++
Cathartes melambrotus			+
Accipitridae			
Elanoides forficatus			+
Buteo magnirostris (p)		+++	+++
Buteogallus urubitinga	+		
Busarellus nigricollis	++	++	
Falconidae			
Daptrius ater (p)		++	++
Daptrius americanus (p)			+
Milvago chimachima		++	
Falco rufigularis (p)			+
Cracidae			
Ortalis guttata		++	++
Rallidae			
Aramides cajanea		+	
Eurypygidae			
Eurypyga helias (p)		+	+
Jacanidae			
Jacana jacana	++	+	
Charadriidae			
Charadrius collaris	+		
Scolopacidae			
Tringa flavipes	++		

TABLE 1 (*cont.*)

	Zone		
	Lower	Middle	Upper
Tringa solitaria			+
Actitis macularia			+
Laridae			
Phaetusa simplex	++		
Sterna superciliaris	+		
Columbidae			
Columbigallina talpacoti	+		
Psittacidae			
Ara ararauna (p)			+
Brotogeris versicolorus		+++	+++
Amazona sp.		+++	+++
Cuculidae			
Piaya cayana		++	++
Crotophaga major (p)	++	++	
Crotophaga ani	+++	+++	
Strigidae			
Otus choliba		+	
Caprimulgidae			
Nyctidromus albicollis		+++	+
Trogonidae			
Trogon viridis			+
Trogon collaris		++	++
Alcedinidae			
Ceryle torquata	+++	+++	
Chloroceryle amazona	++	+++	++
Chloroceryle americana (p)		+	++
Momotidae			
Momotus momota		+	
Galbulidae			
Galbalcyrhynchus leucotis		++	+
Galbula cyanescens		++	++
Bucconidae			
Monasa nigrifrons		++	+
Chelidoptera tenebrosa (p)	+	+++	+++
Capitonidae			
Eubucco richardsoni			+
Ramphastidae			
Ramphastos tucanus		++	+++
Pteroglossus castanotis		++	+++
Pteroglossus inscriptus			+
Picidae			
Melanerpes cruentatus		++	
Phloeoceastes melanoleucos			+

TABLE 1 (*cont.*)

	Zone		
	Lower	Middle	Upper
Dendrocolaptidae			
Xiphorhynchus sp.		+	++
Furnariidae			
Furnarius leucopus		++	+++
Formicariidae			
Pygiptila stellaris		+	
Cotingidae			
Cotinga sp.			+
Tityra sp.		+	
Tyrannidae			
Colonia colonus			+
Arundinicola leucocephala	++		
Pyrocephalus rubinus	++	+++	+++
Ochthornis littoralis		++	+++
Tyrannus melanocholicus (p)	+++	++	
Pitangus sulphuratus (p)	++	+++	+++
Hirundinidae			
Tachycineta albiventer	+++	+++	+++
Atticora fasciata	++	++	++
Stelgidopteryx ruficollis	+++	++	+
Corvidae			
Cyanocorax violaceus			++
Troglodytidae			
Thryothorus coraya		+++	++
Mimidae			
Donacobius atricapillus (p)		+++	++
Coerebidae			
Coereba flaveola		+	
Dacnis cayana			+
Dacnis lineata			+
Thraupidae			
Chlorophonia cyanea		+	+
Tanagra laniirostris			+
Tangara chilensis			++
Ramphocelus carbo	++	++	+
Cissopis leveriana			+
Icteridae			
Psarocolius sp.		++	++
Cacicus cela		++	
Icterus icterus		+	
Agelaius icterocephalus	++		
Fringillidae			
Saltator coerulescens		+	
Paroaria gularis (p)		+++	+++

TABLE 1 (*cont.*)

	Zone		
	Lower	Middle	Upper
Sporophila castaneiventris		++	
Myospiza aurifrons		+	
Total	26	57	58
Combined Total		88	

three swallows, and one tanager) whose distribution was largely independent of the character of the vegetation, the lower zone was found to share relative few species with the middle zone and none at all with the upper zone.

It was apparent moreover that the waters of the lower Callaria are ecologically distinct from those of the nearby Ucayali. The most striking evidence for this distinction was provided by the distribution of the river cormorant, *Phalacrocorax olivaceus*, which occurred on the Ucayali in flocks of thousands but was altogether absent from the Callaria. Three other common species of the Ucayali, *Casmerodius alba*, *Phaetusa simplex*, and *Sterna superciliaris*, appeared on the Callaria only in the immediate vicinity of its mouth, and there in sparing numbers.

(2) As could be expected, the middle zone is faunistically the least distinct of the three. It showed the lowest proportion of characteristic species (26 per cent). Thus our impression that the middle zone is a region of vegetational transition between the flood plain scrub habitat and the upstream forests is confirmed by the distribution of bird species in the three regions.

It will be noted in Table 1 that the middle zone was the only one in which all three species of kingfishers were found. *Ceryle torquata*, *Chloroceryle amazona*, and *C. americana* form a graduated series from large to small, respectively. The distribution of the three species was closely correlated with the width and swiftness of flow of the Callaria. *Ceryle torquata* was the most abundant form along the lower section, while *Chloroceryle amazona* was more common in the middle zone where the river is narrower and faster. The smallest kingfisher, *Chloroceryle americana*, was infrequent in the middle zone but was found with *C. amazona* in equal numbers on the sheltered and rapidly flowing water of the upper zone.

(3) The upper zone, though sharing 43 per cent of its avifauna with the middle zone, nevertheless had the highest proportion (38 per cent) of characteristic species. Thus, as a natural habitat the forest can be shown to offer more opportunities for ecological specialization than the habitats in the two downstream zones. In fact, apart from the wide-ranging species found over the river the fauna of the upper zone appears to be entirely distinct from that of the lower zone.

TABLE 2
ZONAL DISTRIBUTION OF BIRD SPECIES ON THE RIO CALLARIA.

Zonal distribution of species	Lower zone		Middle zone		Upper zone	
	No. of species	Per cent of total	No. of species	Per cent of total	No. of species	Per cent of total
Observed in all zones	11	42	11	19	11	19
Only in upper and middle	—	—	25	44	25	43
Only in middle and lower	6	23	6	11	—	—
Only in upper and lower	0	0	—	—	0	0
Only in one zone	9	35	15	26	22	38
Total	26	100	57	100	58	100

(4) It is evident that overall species diversity is promoted to a much greater extent by the more complex multi-storied vegetational structure of the upper and transitional zones than by the flood-plain scrub of the lower zone.

(5) The fact that the three zones shared in common only 11 species of birds suggests that ecological specialization may have played a major role in the development of the strikingly rich neotropical avifauna.

Our list of 88 bird species undoubtedly represents no more than 30 per cent of the total number that occur in the vicinity of the Rio Callaria. However, our observation time was fairly evenly divided among the three zones, and there are no outstanding reasons for supposing that any of the faunal samples we obtained are not representative. Thus it seems safe to assume that a more thorough-going study would only strengthen our conclusions, though at the quantitative level alteration of the results would be expected.

FEEDING ASSEMBLAGES

While on the Callaria we located two fruiting trees in which large and heterogeneous groups of birds had assembled for the purpose of feeding. The birds using each of these trees were observed for several periods of 1–2 hours. The first tree (see Table 3 for list of bird species observed in it) was located about 100 yards from the Rio Callaria in second growth near an Indian village and bore many brown plum-sized fruits. The second tree (see Table 4 for species list) overhung the Rio Callaria from the edge of tall upper-zone forest, and was heavily laden with orange cherry-sized fruits. A striking fact evident from the tables is that these two feeding trees contained no species in common. The first tree (Table 3) had a broad crown about 40 feet high and stood in dense second growth in the transitional zone near an Indian village. A much taller primary forest was less than 100 yards away, however. The second tree (Table 4) was located on the river bank in the primary forest upstream and was more than twice as tall as the first.

Table 3
List of Birds Observed in First Fruiting Tree.

Brotogeris versicolorus	*Coereba flaveola*
Piaya cayana	*Psarocolius* sp.
Galbalcyrhynchus leucotis	*Cacicus cela*
Melanerpes cruentatus	*Icterus icterus*
Dendrocolaptidae sp.	*Sporophila castaneiventris*
Tityra sp.	

A second fact apparent from the tables is the large number of families represented in both feeding assemblages. The 11 species found in the first tree represent nine families, while the 17 from the second tree include 10 families. Similarly, Land (1963) recorded members of 11 families of birds taking fruit from a tree in Guatemala. The association of diverse species possessing a wide variety of sizes and bill shapes in feeding trees suggests extensive niche overlap among carpophagous birds in the neotropical forests. It is evident that birds so conspicuously different from one another as chachalacas, parrots, toucans, and honeycreepers at least occasionally utilize the same food sources. Though tropical species are usually assumed to be more specialized and less versatile than their counterparts in higher latitudes (Klopfer, 1962; Margalef, 1963), the congregation of large numbers of disparate species at ephemeral food sources suggests that many of them may have rather flexible feeding habits.

In observing the second tree (Table 4), we noticed that the individuals of certain species were distributed in a non-random fashion. Trogons (*Trogon collaris* and *T. viridis*) kept to the lower branches, while the toucan, *Ramphastos tucanus*, the honeycreeper, *Dacnis cayana*, and the tanager, *Tangara chilensis*, were seen only in the upper branches. Other species, e.g., the chachalaca, *Ortalis guttata*, and the *Pteroglossus* toucans, appeared to feed indiscriminately in the lower, middle, and upper branches of the crown. As MacArthur (1958) has so carefully shown for 5 species of *Dendroica* warblers in a Maine spruce forest, interspecific competition for food is greatly reduced in species having pronounced preferences for different locations in the canopy.

In general, birds arrived at and left both fruiting trees as individuals or else as groups of several individuals belonging to one species. The majority of species was seen to come and go in this manner. Although the species composition of these assemblages changed gradually with time, the total number of birds in a given tree did not vary by more than a factor of two during the observation periods. The largest movements were the arrivals and departures of small groups of parrots or toucans. Thus the congregation

TABLE 4
LIST OF BIRDS OBSERVED IN SECOND FRUITING TREE.

Ortalis guttata	*Phloeoceastes melanoleucos*
Amazona sp.	*Cotinga maynana*
Trogon collaris	*Cotinga cayana*
Trogon viridis	*Cyanocorax violaceus*
Capito sp.	*Dacnis lineata*
Ramphastos tucanus	*Dacnis cayana*
Pteroglossus castanotis	*Tangara chilensis*
Pteroglossus inscriptus	*Ramphocelus carbo*
	Cissopis leveriana

of birds that are attracted to fruit trees for feeding cannot be regarded as flocks in that they do not appear to have any social or temporal integrity. Rather, they may be considered as transient and more or less chance assemblages of small flocks of several species plus scattered individuals of others. Socially organized itinerant feeding flocks of the kind extensively described by Davis (1946), Short (1961), and Moynihan (1962) are of widespread and common occurrence in neotropical forests. Such true flocks differ from feeding assemblages in the following respects. (1) They are characterized by interspecific social interactions rather than by the lack of them. (2) They retain their integrity as social units while progressing through the forest. Feeding assemblages of necessity are stationary. (3) Members of a feeding flock pursue a variety of food sources, both plant and animal, while in a feeding assemblage all individuals are consuming the same food.

It can be expected that members of feeding flocks may temporarily join feeding assemblages and that birds initially in feeding assemblages in turn may leave to join feeding flocks. Such exchanges could have taken place in the second feeding tree during our observations, as birds of the genera *Dacnis* and *Tangara* are known (Moynihan, 1962) to join feeding flocks.

SUMMARY

1. The distribution of birdlife along a 20–30 mile section of the Rio Callaria (Department of Loreto, Peru) has been tabulated with reference to three conspicuously distinct ecological zones, through which one passes in succession when travelling upstream from the mouth. They are characterized by differences in the width and rate of flow of the stream and by the principal features of the vegetation on the banks. The ecological character of the zones has been analyzed by considering the proportions of the fauna of each which occurred in only that zone and in the two other zones. The degree of faunal distinctness and the pattern of faunal overlap with other zones was different for each zone. As expected, greater species diversity was found in the zones of greater vegetational complexity.

2. Two fruiting trees which were being used for feeding by representatives of nine and ten bird families, respectively, have been described. The significance of the high diversity of bird species using these feeding trees has been discussed. Accompanying behavioral observations have been considered in relation to the problem of interspecific competition. Assemblages of birds using such feeding trees have been operationally distinguished, on the basis of three behavioral criteria, from the itinerant feeding flocks, so prevalent in neotropical forests, that recently have received much attention from other authors.

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LITERATURE CITED

Davis, D. E.
1946 A seasonal analysis of mixed flocks of birds in Brazil. *Ecology*, 27:168–181.

de Schauensee, R. M.
1966 The species of birds of South America and their distribution. Acad. Nat. Sci., Philadelphia, Pennsylvania.

Klopfer, P. H.
1962 Behavioral aspects of ecology. Prentice-Hall, Inc., Englewood Cliffs, N. J.

Land, H. C.
1963 A tropical feeding tree. *Wilson Bull.*, 75:199–200.

MacArthur, R. H.
1958 Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39:599–619.

MacBride, J. F.
1936 Flora of Peru. *Publ. Field Mus. Nat. Hist., Bot. Ser.*, 13, Part I, No. 1.

Margalef, R.
1963 On certain unifying principles in ecology. *Amer. Nat.*, 97:357–374.

Moynihan, M.
1962 The organization and probable evolution of some mixed species flocks of neotropical birds. *Smithsonian Misc. Publ.*, 143:1–140.

Short, L. L., Jr.
1961 Interspecies flocking of birds of montane forest in Oaxaca, Mexico. *Wilson Bull.*, 73:341–347.

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